

PAIRING BEHAVIOR OF PIGEONS RELATED TO
AGGRESSIVENESS AND TERRITORY

by

PAUL LOUIS CASTORO

A. B., San Jose State College,
San Jose, California, 1948

A THESIS

submitted in partial fulfillment of the

requirements for the degree

MASTER OF SCIENCE

Department of Zoology

KANSAS STATE COLLEGE
OF AGRICULTURE AND APPLIED SCIENCE

1950

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INTRODUCTION

During the past decade emphasis has been centered upon individual aggressiveness in studies of the behavior of animals. This aggressiveness seems to play an important role in various societies of vertebrates in that it may lead to the establishment of ranks within a specific group. An individual of high rank in his particular group usually has a precedence in obtaining food, territory and a mate.

According to Collias (1944), aggressiveness may be expressed in two forms, (a) hierarchies of precedence within a social group and (b) the defense of a territory. In defining the word, aggressiveness is the self assertiveness of an individual usually shown by fighting, nipping, pecking or bluffing. In various species of birds this aggressiveness may be shown in two ways. According to Schjelderup-Ebbe (1935), a peck-right system was observed in various flocks of fowl, especially the domestic chicken. This peck-right may be defined as the pecking of a subordinate bird by a superior bird with no return of pecks by the subordinate. The second way that aggressiveness may be shown was that observed by Bennett (1939) in her studies of ring doves. She concluded that a social hierarchy was established by a peck-dominance and not a peck-right as described by Schjelderup-Ebbe. Peck-dominance is described as the condition in which two individuals, irrespective of rank, exchange pecks, first one retreating and then the other. The one delivering

the greatest number of pecks is said to have peck-dominance for that pair.

Nice (1941) and Howard (1920), in their observations of birds in the wild, noted that a bird holding a given territory usually drove out an invading bird regardless of the dominance-subordination relationship between them. The concept of territory as generally described is regarded as that area which is defended by an individual and used in either or all of the following: feeding, mating, rearing of young and roosting. In birds which flock close together, such as pigeons, the size of the territory is usually very small and an asymmetric peck-exchange is usually present. This peck-exchange has been called "peck-dominance" by Masure and Allee (1934). When territorial relations are involved it is difficult to determine which individual is most aggressive, since the less aggressive individuals tend to remain in their own territory, where they are victorious in most of their fights.

The territory, courtship display, premating display and other behavior patterns in pigeons has been discussed to a great extent in the classic works of Charles Otis Whitman (1919), and also in work done by Craig (1918) and Gifford (1941). Courtship display in pigeons is usually performed by the male and shown by the puffing of the breastfeathers, dragging of the tail, cooing, and treading of the feet on the floor. If the female is receptive she will nod her head, after which billing will follow. Billing is the act in which the male presents an

open beak into which the female inserts her own. There is evidence that the male regurgitates into the beak of the female. After billing, the female will crouch, elevate her wings and receive the male in copulation.

In reviewing literature on mating behavior in birds, it was noted that the social status of an individual bird may have a definite relationship to mating. Guhl, Collias and Allee (1945) showed that a dominant male chicken possessed a greater freedom to mate than did the socially inferior males of a flock. In another experiment to determine whether the social dominance of males over females exerted any influence on success in mating, Guhl (1949) found that social dominance of the males over the females was not essential for treading and copulation although it did facilitate mating. Observations of unisexual matings among hens or cocks also suggested that the bird assuming the male role was more successful in mating with its social inferiors than with its superiors.

In the experiments cited above, reference was made chiefly to birds that are polygamous. In the experiment reported in this paper, an effort was made to determine the influence of aggressiveness (both in a neutral area and in a territory) on mate selection in pigeons which practice monogamy. Pigeons were also selected for this experiment due to their lack of dimorphic characteristics, in which some hidden factor other than secondary sex characteristics (morphological) which might play a part in mate selection. It was then hypothesized that

in a monogamous bird, such as the pigeon, aggressiveness of an individual may bear some direct relationship in mate selection. The experiment was set up with the consideration of the lack of territory in pair formation and then with the consideration of a territory in which it has been shown the bird is dominant.

EXPERIMENTAL METHODS AND PROCEDURE

The pigeons used in this study, termed as commons by the layman, were obtained from a farm house close to the Kansas State College Campus in Manhattan. The generic and mating background of these birds was not known and was thought to be of little importance in an experiment of this particular nature. Of the 45 birds trapped 26 (both males and females) were selected on the basis of equality of size and the appearance of the general body condition which would indicate good health. These birds were brought into the laboratory and each was treated with five percent Chlordane powder to eliminate the possible spread of ectoparasites to other animals which were also housed therein.

The next procedure was the determination of sex, which proved to be quite a task, for pigeons are monomorphic, that is, they do not show any of the usual differentiation in secondary sex characteristics as do many species of birds. The method used in sexing was similar to that described by Lee (1915) which is basically as follows: the male pigeon is usually

larger and heavier than the female. The pelvic bones in the male appear to be close together and hard, while in the female they are usually spaced further apart and are soft. Mr. Herman Smith, research assistant of the Poultry Department at Kansas State College, helped sex these birds, and he noted that semen may be "milked" from the cloaca in some of the males, although this did not hold true in all cases.

The most positive method of sexing the birds was by observation of the behavior patterns that are indicative of the male of the species. It is generally known by persons who are familiar with pigeons that the male's behavior is quite different from that of the females. In approaching an individual, a male pigeon will puff up his neck and breast feathers, spread and drag his tail feathers on the ground and start to coo in a loud voice. He will usually bob and weave his head, while at the same time his feet are tramping on the ground. On the other hand, the female will puff up her neck feathers very slightly and may use her voice which is quite mild in comparison with that of the male.

The birds in this experiment were placed in a small cage and observed for a period of two days. As male behavior was noted in a bird, he was immediately placed in a cage along with other males. The females were also placed, as they were identified, in a cage far removed from that of the males.

The next step was banding of the birds so that records could be kept on each individual. They were banded with stand-

ard type pigeon bands, using a red colored band for the males and a green colored band for the females. The range of numbers, on the bands, in the males was from 1 to 13 inclusive, and in the females they ranged from 12 to 25.

The Home Cage

On the completion of sexing and banding the males and females were kept in separate cages each measuring 6' x 4' x 2'. In these cages were food and water, perches, and grit to help sustain a healthy condition of the pigeons. Although there was very limited space, the birds moved about quite freely but could not fly. It was found that in using such a cage, the problem of catching the birds desired was greatly simplified.

In the male cage there was usually a scene of constant turmoil. There were many fights over roosting and feeding sites which suggested that territorialism was being set up. On attempting to catch a bird for experimental use, it was noted that one was able to find the desired bird in the same area repeatedly. This was interpreted as territorialism even though the boundaries of the areas were quite indistinct to the observer.

The cage containing the females, on the other hand, was usually very quiet with only an occasional contact occurring in the flock. These pigeons usually were scattered indiscriminately in the home cage and were never found in any particular

area. This indicated that the females probably did not set up territories in this cage.

The home cage served as a place for housing the unisexual groups during the experiment. The reason for keeping the birds in unisexual flocks was to allow the birds to forget their former mates (in the wild). According to Carpenter (1933), it took pigeons about 24 days to forget their mates. To insure complete loss of recognition of former mates, the sexes in this study were kept apart for a period exceeding 40 days.

The Combat Cage

In this study, a new approach was used to test the relative aggressiveness of pigeons, the principal idea being to remove the factor of territory by placing two birds in close contact within a neutral area. This was facilitated by the use of a small circular cage with the diameter of 13 inches and a height of 8 inches. The small size and shape of this cage allowed the birds to be intimately close at all times with no corners in which to seek refuge or avoidance.

Two pigeons of the same sex were removed from their home cage and introduced simultaneously into the combat cage. The observer then retired behind a screen so that his presence would not be observed by the birds. After a short time, the males usually began to fight, but females, being less pugnacious, had to be stimulated by competition for food. This was accom-

plished by the removal of food from the home cage for a period of 24 hours prior to introduction into the combat cage. In running the tests, of females, a small container of food, fastened to the floor of the combat cage, usually evoked a fight between the two females involved. The results of these tests for relative aggressiveness will be given later.

The Pairing Cage

After the females were ranked according to the number of fights each won, i.e., their relative aggressiveness, they were tested by pairs with a single male. The object of this test was to determine whether the male would pair more readily with the more or the less aggressive female.

The cage used in this test was circular and approximately two feet in diameter and one foot in height. It was constructed of the standard type of chicken wire fastened to a wooden floor. Two females and one male were introduced at the same time through the trap door at the top of the cage and observations were made as to which female was chosen by the male.

The Flight Cage

Once the pairings as observed in the pairing cage were completed, the males were introduced into a new cage. This cage (flight cage) was the largest used in this study; the

dimensions were 6' x 5' x 7'. It was constructed of standard chicken wire on two sides, 10 nest boxes comprised the third side and the wall of the building served as the fourth. The flight cage was amply supplied with perches, food and water containers and flight and ground areas. The nest boxes were labeled with letters ranging from A to J inclusive; the letter K was used to designate the floor space directly beneath the bottom tier of nesting boxes. In lettering the nest-boxes in this manner, it simplified the task of rapid tabulation during the periods of observation.

Once the males established their territories in the flight cage, the females were introduced. First the females were introduced singly. When pairing was effected, the female being tested was returned to the home cage. When a female was removed, the males were given one or more days to rest and feed before another female was introduced. Later the whole female flock was introduced as a group and subsequent pairings were noted.

OBSERVATIONS AND RESULTS

Determination of Relative Aggressiveness

To determine the relative aggressiveness in both sexes of pigeons, the birds were brought together as unisexual pairs in the combat cage as described. Behavior indicative of superiority or dominance was noted and recorded.

The observational technique used to determine the victor of a contest was as follows:

The Males. As had been stated, the males needed no stimulation to start a fight. Once placed in the combat cage, display by one bird usually started immediately. This display, consisting of puffing up of the feathers of the neck region, dragging of the tail feathers on the floor treading of the feet and loud vocalizations, was usually resented by the other male in the cage. The male which did not display, either attempted immediately to escape from the displaying male, or he resisted by directing a series of pecks toward the displaying bird. The former type of behavior was designated as a "no fight" type of contact. Evidently this type of behavior may have been a carry-over or recognition of the dominance-subordination relationship established in the home cage. The bird that showed the avoidance reaction was considered to be the loser in that particular contact.

The second type of contact, designated as a "fight", was observed when the nondisplaying male resisted the advances of the displaying male by the delivery of a series of pecks. This type of action was usually the beginning of a furious fight between the two males. Both birds pecked at each other until one bird began to avoid the pecks of the other and sought a means of escape from the cage. Once this type of behavior was observed, the bird displaying avoidance was considered the loser of the contest. An example of a typical "fight" between

two males (M8¹ and M12) is as follows: As soon as both males were introduced into the combat cage, M8 began to display and chased M12 around the cage. M12 then stopped, turned and delivered two severe pecks at M8's head. Male 8 immediately returned the pecks and a fight ensued. Repeated pecks, wing slaps and loud vocalizations were exchanged during the fight. Finally M8 seized M12 on the neck, established a firm hold, and began to shake M12 in a manner similar to that of a dog shaking a piece of cloth. The position of M12's body was somewhat like a crouch or squat with M8 directly above him. Once released from this grip, M12 began a futile attempt to escape from the vicious onslaught of pecks delivered by M8. In view of this type of behavior, M8 was definitely the victor of this contact.

It was most interesting to note that the body position taken by the subordinate bird was somewhat lower than that of the victorious bird. If the subordinate bird brought his head to the same level as the dominating bird's head, the dominant bird would immediately direct a series of pecks at the other bird with no return of pecks by the inferior bird. This behavior was typical in most of the cases observed in the combat cage.

A "draw fight" was established when both birds fought with no apparent submission by either of two birds. In this case, it was noted that the birds remained facing each other in an

¹In this thesis M denotes male, F denotes female.

alerted attitude, heads held high and body very tense. If one made the slightest attempt to move toward the other, the second bird would immediately pounce on the first thus starting another fight. One pair of birds was observed to remain in this situation for a period of over an hour with no bird yielding to the other.

In some cases there were "no contests", and in these there was no action between the birds. There was no attempt to display, peck or bluff. In many of these cases the birds actually closed their eyes and went to sleep. The observer had no alternative but to record a "draw".

Three rounds of contacts were performed, making a total of 330 contacts for the male group. The birds were fought in a systematic manner so as to fight every possible combination of paired birds. The winner of each contest was recorded and an aggressive order was calculated by awarding the highest position to the bird with the greatest number of contacts won.

Table 1 is a summary of the three rounds of contacts run in the male group. This table was made by tabulating the majority of victories by one individual over another, e.g., Rounds I and III were won by Bird A; Round II was won by Bird B, thus Bird A was selected as being more aggressive than Bird B. The winners are listed vertically on the left side of the table, and the losers to each are listed horizontally. The relative rank of aggressiveness was determined on the basis of the number of contacts won, i.e., M6 won over 10 males and was placed in

top position; M7 won over nine males and was placed in second position, etc. When two or more birds won the same number of contacts, the birds were given the same rank on the aggressive scale.

The Females. Attempts were made to fight the females in the same manner as the males, but the results were, at first, rather unsatisfactory. On placing two females in the combat cage, activity was either very slow or entirely lacking. In order to step up the action, it was necessary to place a small cup of food in the center of the cage and introduce birds which had been without food for a period of 24 hours. This method proved to be highly successful in initiating contact between the birds.

On the introduction of a pair of hungry females into the combat cage, it was noted that both birds fed at the same time until most of the food was gone. The competition over the few remaining grains of food usually stimulated both birds to fight. The fights observed were similar to those described for the males with the exception of the factor of display. The display pattern of the females preceding a fight consisted of slight puffing of the feathers in the neck region and a very mild type of vocalization. There was no treading of the feet or dragging of tail feathers as observed in the males. The terms "fight", "no fight" and "draw" were used, as with the males, to describe the results.

Table 2 gives a summary of three rounds of contacts in the

Table 1. Results of contests between pairs of males in the combat cage. Males are ranked according to number of individuals each defeated.

Winners :	Losers										: Number : defeated :	: Rank
6	7	5	2	3	9	13	1	10	11	8	10	1
7		5	2	3	9	13	1	10	11	8	9	2
5			2	3	9	13	1	10	11	8	8	3
2				3	9	13	1	10	11	8	7	4
3					9	13	1		11	8	5	5
9						13	1	10		8	4	6.5
13							1	10	11	8	4	6.5
1								10	11	8	3	8
10				3					11		2	9.5
11					9					8	2	9.5
8								10			1	11

Table 2. Results of contests between the pairs of females in the combat cage. Females are ranked according to the number of birds each defeated.

Winners:	Losers	: Number : defeated	: Rank
12	14 22 20 18 23 15 21 19 16 17 25 24	12	1
14	22 20 18 23 15 21 19 16 17 25 24	11	2
22	20 18 23 15 21 19 16 17 25 24	10	3
20	19 23 15 21 19 16 17 25 24	9	4
18	23 15 21 16 17 25 24	7	5
23	15 19 16 17 25 24	6	6
15*	21 19 17 25 24	5	8
21*	23 19 16 25 24	5	8
19*	18 16 17 25 24	5	8
16	15 17 25 24	4	10
17	21 25 24	3	11
25	24	1	12
24		0	13

*These birds tied for the same position on the aggressive scale.

female group. The relative aggressive ranks of the females are set up in a manner identical to that for the male group.

The Selection of a Mate Without the Factor of Territory

Once the preliminary work of determining relative aggressiveness was completed, the pigeons were subjected to the second phase of the study. The "pairing cage" was used in this test. In the use of this cage the factor of territory was eliminated. The birds were taken from their respective home cages and introduced simultaneously into a neutral area (pairing cage). The behavior of the three birds was observed and the female with which the male paired was noted. Rank in relative aggressiveness of females was then related to selection by the male.

An example typical of the behavior that occurred in the pairing cage is as follows: Females 12 and 17 were introduced into the cage with male 8. The male immediately started his display, first to F12 and then to F17. This alternating display toward the two females continued for approximately 15 minutes; then the less aggressive of the two females (17) began to signify approval or receptiveness by a bobbing or nodding of the head. This sign of receptiveness was followed by an attempt to copulate, but F12, the more aggressive of the two females, immediately ran to the copulating pair and directed pecks at the female until cessation of copulation was effected. Male 8 again began his display toward F17 which was followed by the

nodding of the head by F17. Copulation was attempted and again broken up by a direct attack of pecks by the unpaired F12. In all, there were four attempts by F17 and M8 to copulate, and each time F12 interfered. About one half hour after introduction into the pairing cage, the first billing between F17 and M8 was noted. After billing, the two birds copulated with no attempt by F12 to interfere. After copulation, preening of the feathers by the paired birds was noted. It was after this billing that the two birds were seen to attack the unpaired female in an attempt to drive her from the cage. When this behavior was noted, the observer removed the three birds from the cage, as it was thought that the two birds had paired and were attempting to establish their territory. Female 17 was chosen by M8 over F12, which was top ranking bird of the female flock.

Each male was introduced to a pair of females until the complete flock of males had been introduced. In many cases it was observed that the superior female maintained an alerted attitude while the inferior female seemed more at ease. This behavior appeared to be of some value in the male's selection of the lower ranking female.

Table 3 shows the results of the pairing tests and has been set up so that one may readily denote the various ranks of the birds involved in each case. Group A is composed of females of various ranks; the females of group B are those of equal rank; group C consists of birds whose ranks are far apart (high-low); the females of group D are high ranking birds; and

Table 3. The results of introducing two females and one male into the pairing cage. The figures in parenthesis indicate the ranks of the individuals in winning fights.

Group:	Male :	Rank :	Dominant :	Rank :	Subordinate :	Rank :	Female
:	:	:	female :	:	female :	:	selected
A	1	(8)	18	(5)	16	(10)	16
	2	(4)	15	(8)	16	(10)	16
	6	(1)	18	(5)	15	(8)	15
	10	(9.5)	14	(2)	19	(8)	19
	11	(9.5)	20	(4)	19	(8)	19
	13	(6.5)	20	(4)	21	(8)	21
	6	(1)	18	(5)	15	(8)	15
	9	(6.5)	23	(6)	24	(13)	24
	13	(6.5)	18	(5)	15	(8)	15
	3	(5)	18	(5)	16	(10)	16
	3	(5)	15	(8)	16	(10)	16
B	13	(6.5)	15	(8)	19	(8)	19
	8	(11)	15	(8)	21	(8)	21
	8	(11)	21	(8)	17	(11)	21
	9	(6.5)	23	(6)	15	(8)	15
	11	(9.5)	15	(8)	21	(8)	21
	13	(6.5)	21	(8)	19	(8)	19
C	3	(5)	21	(8)	23	(6)	23
	6	(1)	12	(1)	25	(12)	25
	7	(2)	14	(2)	25	(12)	25
	9	(6.5)	23	(6)	24	(13)	24
	8	(11)	12	(1)	17	(11)	17
D	9	(6.5)	14	(2)	17	(11)	17
	3	(5)	14	(2)	22	(3)	22
E	5	(3)	22	(3)	18	(5)	18
	3	(5)	16	(10)	25	(12)	25
F	6	(1)	15	(8)	25	(12)	25
	9	(6.5)	15	(8)	24	(13)	24

group E is composed of females of low aggressive rank.

On analysis of the various groups in Table 3, it appeared that the females selected in groups A, C, D and E were the less aggressive of the two females introduced in each test. In group B, however, the females are of equal rank, so the question arises as to which female would be the inferior. According to Table 2, it was observed that F21 defeated F23, yet F23 was placed higher on the aggressive scale on the basis of the number of contests won. The same situation appears in the case of F19 and F18. These observations lead one to believe that a subordinate-dominance situation prevailed and that the male selected the subordinate bird in every case regardless of the ranks in aggressiveness as set up by the writer.

Competition for a Mate and the Influence of Aggressiveness and Territory

The third phase of this problem dealt with the pair formation of pigeons in relation to territory and relative aggressiveness. The entire male flock was introduced into the flight cage where they flew about to investigate the new surroundings. About an hour later the various birds began to select nest sites using, it appeared, the "trial and error" method. At one time a bird would take one nest box and then, for no apparent reason, leave it for another. The birds that had selected a nest box were constantly challenged by the birds without a nest-box. This resulted in the occupant of the box being driven out, or

the challenger's advances were repelled.

The flight cage was a scene of turmoil for about five days. Birds were challenged by non-nest holders, or exchange of nest-boxes between various individuals occurred. On each succeeding day the activity between the males decreased; evidently territories were established and recognized.

Several birds did not take up nest boxes but took up positions on the floor or perches. Males 10, 3 and 9 established their territories on the floor, while M8 established his area on a portion of the perch far from the nest-boxes.

The following diagram shows the nest-boxes (territories)

Nest A M11	Nest B M5	
Nest C M7	Nest D M6	
Nest E M2	Nest F M13	----perch level
Nest G M1	Nest H	
Nest I	Nest J	
Nesting Area K		
M3	M9	----floor level

taken up by the birds. The nest-boxes were lettered to avoid confusion with the bird's legband numbers. There were 10 nest boxes lettered from A to J, and the area on the floor immediately below the tier of nest-boxes was designated as K.

The males at the high positions of the aggressive order acquired nest-boxes at (or near) the average flight level of the cage. In this cage the flight level was presumable at the perch level. The males low in the order established territories on the floor of the cage.

Once the territories had been firmly established by the males, a single female was introduced into the flight cage. After pairing behavior was noted and confirmed, the female was removed. The males ate scantily during the time the female was in the cage and were unusually active; therefore, they were allowed to recuperate for a period of three days after the female was taken out. After this rest period another single female was placed in with the males, pairing behavior was noted, and then she was removed from the cage. This cycle was continued until each female had been introduced to the male flock.

An example of the behavior that followed on introduction of a female to the male flock can be shown when F19 was introduced. As soon as F19 was placed in the cage, she flew to a perch and was approached by M10 which pecked her and displayed. She then flew to nest-box B and was followed by M6 who also attempted to court. The occupant of nest-box B, M5, immediately flew to the box and drove out M6 and began to court the female. M6 re-

entered the nest-box and pecked at the female and forced her out. At this time most of the males were flying wildly about the cage and attempted to attract the female by their display. Fights ensued between the males with the final result that M6 defeated every bird that attempted to court the female. Once M6 dominated the situation, he turned his attention to F19 and began to display to her. F19 then entered various nest-boxes followed by M6 who would drive her out by pecking. F19 returned to the perch while M6 went to his own nest-box. Here he began his call to the female in an attempt to induce her to his nest. The female evidently did not recognize his call; so he began to fly repeatedly between the nest-box and the female which appeared to be an attempt to indicate the position of his nest-box. When she ignored these actions, M6 flew to her and began to peck her in an attempt to drive her to the nest. M6's behavior in this attempt to drive the female to his box was very interesting. He pecked her on the head, bumped her with his breast, and even grasped her neck feathers with his beak and tried to pull her to his nest. When this failed, he repeated his flights to the nest box and back to the female as described above. Each time on entering his nest, M6 used vocalizations which has been interpreted by Whitman (1919) as a method by which a male summons his mate to the nest.

Once the female reached the nest, M6 began his courtship display. This display consisted of the male circling the female while she sat in the center of the box. Her position was

similar to that of an incubating female sitting on eggs. Then he pecked gently at the female's head which resulted in a trembling wing motion in the female quite similar to that of young pigeons begging the parents for food. Then the situation reversed with the male sitting and the female circling and pecking his head. At times it appeared that the bird actually rubbed its head on the sitting birds neck. This action was followed by preening each other's feathers in the neck and head region. Billing immediately followed and copulation occurred.

Once the pair had copulated, the female would aid the male to drive out any intruder that attempted to gain access to the nest-box. This is significant in that it shows that the female had assumed a partnership in defending the territory. At this point the female was removed from the cage.

The results of the pairings in the flight cage are shown in Table 4. It was noted that the most aggressive male (M6) paired with almost one half of the females introduced in the cage. The male in second position of the aggressive scale (M7) paired with three females, and M5, the third highest ranking male, received one female. In totaling the number of pairings by the three highest ranking males, it was found that they paired with nine females introduced into the flight cage. Also of significance was the fact that the lower ranking females paired within two days while the higher females required from five to nine days to pair.

Table 4. Results in placing females singly into the flight cage.

Rank of male	Male : number :	Females selected						
1	6	25	21	19	14	17	12	
2	7	23	18	15				
3	5	24						
4	2							
5	3	20	22					
6	9							
7	13							
8	1							
9	10	16						
10	11							
11	8							

Introduction of the Flock of Females to the Male Group

In the final phase of this experiment, the entire flock of females was introduced to the males in the flight cage. Then through observation of the behavior which followed, the writer attempted to tie up the results obtained in preceding tests.

All the females were placed in the flight cage except F12. This bird was disqualified for she had been in the flight cage with the males two days prior to the commencement of this last test. It was believed that she would immediately return to the male with which she had previously mated. As the females entered the cage, the males immediately started to fly wildly about and began to display vigorously. The males pursued the females from the nest-boxes and perches and violated each others territorial rights. The females flew from nest-box to nest-box

in which the occupant (male) displayed. The top ranking male (6) displayed to a great number of females at various intervals and never centered his attention on any particular female. Meanwhile, the other males appeared to single out specific females and displayed to them. At the end of the second day, it appeared that the females had chosen a nest-box by chance, for they did not appear to heed the displays of the males. There was so much noise during the first two days that the observer could not ascertain if a given female was reacting to the call of a particular male.

On the third day, the noise and commotion in the flight cage had subsided considerably, and it was found that a great number of females and males apparently had paired. A female and a male pigeon were observed to be together in many of the nest-boxes and premating behavior as described in the third phase of this problem was noted. The top ranking male (6) was still pursuing the unpaired females and did not appear to focus his attention on any particular female. Male 5 was driven from his original nest-box (B) by a concerted attack of F17 and M8; so he assumed possession of the unoccupied area K with F22.

Four days following the introduction of the females the following birds appeared to be paired, F15 and M11, F17 and M8, F18 and M7, F25 and M1, F20 and M2, F22 and M5, F16 and M10. Female 19 was noted to act quite aggressively in that she pursued F21 from M13 and M6. If F21 joined M6 in his nest-box, F19 would leave M13 and fly to M6's box and drive her out.

After this, F19 remained in M6's nest-box until she saw F21 enter M13's nest. She then flew down to the box and again drove out F21 and remained with M13. The behavior of F19 to defend the nest-boxes of two males against F21 was observed until the fifth day. On entering the laboratory on the sixth day, the observer noted that she had paired with M13 leaving F21 with M6.

Female 14, the top ranking bird of the female flock since F12 had been eliminated, was without a male until the end of the fifth day. On the sixth day she had set up a nest site under the feed trough with M3. Male 9 and F23 were without a definite territory at this time, but pre-mating behavior was observed between them on a perch.

On the seventh day the birds had settled down and the males were observed to carry straw from the floor of the cage to the nest-boxes which was an indication that pairing was achieved and nest building was in progress. Female 23 and M9 had moved from the perch to nest-box I and showed signs of further pre-mating behavior. Female 16 had laid an egg at the end of the sixth day and was observed incubating it on the seventh day. Female 14 and M3 had moved from their site under the feed trough to a box placed on the floor opposite the tier of nest-boxes where they had established a territory.

Table 5 shows the pairing that resulted in the flight cage when the females were introduced to the males. The time (in days) is recorded to show approximately how long it took for

Table 5. Pairs formed after the introduction of the females, as a group, into the flight cage containing the males.

Day :	Male		:	Female	
	Number	Rank		Number	Rank
1	8	(11)		17	(10)
	11	(9.5)		15	(7)
	10	(9.5)		16	(9)
2	2	(4)		20	(3)
	1	(8)		25	(11)
3	7	(2)		18	(4)
4	5	(3)		22	(2)
5	13	(6.5)		19	(7)
	6	(1)		21	(7)
6	9	(6.5)		23	(5)
	3	(5)		14	(1)

the various birds to pair. The relative aggressive rank of each bird is shown in parenthesis, but in the females, due to the absence of Fl2, the ranks of each bird has been raised one position higher than shown in Table 2.

The trend appeared to be that the males paired with those females which approximated their ranks of aggressiveness. A divergence from this trend was found in the case of M6, the top ranking male, in which he mated with a female in seventh position. Female 24, the lowest ranking female, was left without a mate.

The time factor in these pairings was noteworthy in that it appeared that the males and females of high rank took a greater period of time to mate.

DISCUSSION

This experiment which focused on the factor of aggressiveness in pair formation has indicated that (a) both sexes of pigeons may be ranked through contests in the combat cage, (b) in the procedure used in the pairing cage, the males selected the subordinate of the two females introduced, (c) high ranking males are most successful in pairing with a single female introduced into the flight cage and (d) females introduced as a flock into a pen of males may pair with any individual.

In some preliminary tests which were used to test the reliability of the combat cage technique, the pigeons were ob-

served in their respective cages at various intervals. The contacts between the various individuals were noted and later compared to those in the combat cage. The dominance-subordination status of the birds observed in the flock confirmed the results obtained in the combat cage.

On analysis of Table 3 with reference to the actual contacts shown in Table 2, it appeared that the male selected the subordinate female of the two introduced into the pairing cage. According to Collias (1944) the sex invitation (or crouching behavior) by the female is considered in part as submissive behavior. Just how this submissive behavior by the female pigeon is recognized by the male is not clearly defined, but the writer assumes that body position by the submissive female may play an important part. In running the tests in the combat cage, it was noted that the submissive bird usually assumed a crouching or lower body stance than that of the dominant bird. In the pairing cage, however, the observer could not detect any posturing which denoted submission. It is probable that a male could recognize the lower body position of an inferior female. The dominant bird in the pairing cage had a definite alerted attitude which may also be indicative of dominance to the other birds.

Results of Table 4 indicated that there is a relationship between the aggressive rank and precedence for mating, because a high ranking male bird usually paired with a single female introduced to a group of males. The three highest ranking males

paired with nine out of 12 females introduced in the flight cage. Precedence in mating was found by Guhl, Collias and Allee (1945) and by Guhl and Warren (1946) in their observations in the domestic fowl. High social rank in a dominance order has been related to greater freedom in territory selection and mating for a number of vertebrates such as fish (Greenberg, 1947); lizards (Evans, 1938; Greenberg, 1943); birds (Nice, 1941); monkeys and apes (Carpenter, 1942).

It was noted during the introduction of the top ranking females that the pairing time was longer than those of lower rank. Although the males attempted to pair, the high ranking females appeared hesitant and showed little inclination to pair with any male when first introduced into the flight cage. Schjelderup-Ebbe (1935) noted that high social rank in domestic hens interfered with mating. Guhl (1949) substantiated this observation by experimentation.

Although the data are insufficient to render a definite statement about the pairings which occurred when the entire flock of females was introduced to the males in the flight cage, a trend appeared in the results as shown in Table 5. This trend seemed to indicate that the birds which paired were those of approximate ranks. The only cases in which this did not occur were those of the top ranking male and the lowest ranking female. The top ranking male did not seem to center his attention on any particular female, consequently, the females were taken up by other males. The incident between F19 and F21

possibly hindered M6 from mating much sooner than he did. Female 24 remained unpaired; this was probably due to her low aggressive rank in the female flock.

An interesting factor, observed in tabulation of the data, was the amount of time required to mate in relation to the aggressive ranks. It appeared that those of inferior and intermediate ranks paired in a shorter time than those birds of high ranks. The reason for this is not clear, but it was thought that the females of high rank were avoided by the males, and the male of top rank attempted to court too great a number of females with no specific female receiving his full attention.

On the basis of actual observation of the mixed flock, it appeared that the commotion which occurred on introduction of the females to the males caused the females to fly into the empty nest-boxes to avoid the confusion. The male occupant of the nest-box immediately flew to her and began to display. If a second male bird flew to the nest-box to court the female, the occupant, being dominant in his own territory, drove him out. This type of behavior lead the observer to believe that this pair-formation was one of chance. Tabulation of the ranks of each bird (male and female) that paired also seemed to indicate chance pairing due to the fact that the males were of high ranks and females low in three pairs, in five pairs the female ranks were higher than those of their mates, and in three pairs the ranks of the mates were almost equal.

It was found that this new technique used in determining

the aggressive ranks in pigeons proved to be satisfactory as it gave consistent results in most cases. The aggressive position of each bird was calculated without the interaction of territory and aggressiveness as found in established flocks. This new method gave the observer an accurate record of each birds true aggressive rank.

Under natural conditions the factors of relative aggressiveness and territory may operate concurrently during pairing behavior. The technique of this experiment has tested these two factors separately and found that each exerted an influence on mate selection. The results obtained from the pairing cage and from the flight cage when females were introduced singly would suggest that chance pairings might not have been as numerous as those occurring in the final results of this experiment. Under free-ranging conditions the birds would have had more space and probably less vigorous interactions; and pairing would most likely not have occurred simultaneously as the individuals would presumably vary in the phases of the reproductive cycle. A repetition of this experiment with a larger flight cage, and probably other modifications, may be profitable.

SUMMARY

1. The relative aggressiveness of both sexes of pigeons was determined by use of the combat cage. This cage eliminated the factor of territorialism and also served to bring two birds

in close contact with each other to encourage fighting. Rankings of relative aggressiveness within each sex was determined by the number of contests won by each.

2. An attempt was made to determine which of two females a male would select as a mate without the factor of territory. It was found that he selected the subordinate female of the two introduced into the cage. The criteria for determining when pairing was effected were those of billing, copulation and establishment of territory in the pairing cage. Both birds that had paired were observed to drive out the unpaired female.

3. A single female was introduced to a flock of males in a flight cage to find which male would pair with her. The males had already established territories, the most aggressive selected the best nest-boxes. It was found that the males ranked high on the aggressive scale usually mated with the females introduced in the cage. It was also noted that the more aggressive females took a longer period of time to mate than the less aggressive females.

4. The whole flock of females were introduced to the male flock in the flight cage. Pairing was noted and it was found that the pairs formed showed no definite relationship as to rank. It was also noted that the birds of lowest rankings seemed to pair off more readily than those of high rankings.

ACKNOWLEDGMENT

Indebtedness is expressed to Dr. A. M. Guhl, Associate Professor of Zoology, for suggesting the problem and for his counsel during the course of the experiment; to Herman D. Smith, research assistant in poultry husbandry, who suggested the use of the combat cage and aided in the observations of the pigeons; and to C. L. Miller, graduate assistant in zoology, for aid in carrying out various phases of the experiment.

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